Chapter 14

The Present and Future of Insect Life-Cycle Evolution

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14.1 Introduction

The symposium in Vancouver and the chapters in this volume provide a diverse array of studies on insect life-cycle evolution. This array can be broken down into at least three levels of approach: (a) comparisons of genetic variation and covariation underlying life-cycle traits; (b) comparisons of variable phenotypes within and among populations of the same and/or related species; (c) comparisons of habitat-specific traits regardless of relatedness.

The first approach recognizes first that, for selection to affect a trait in a population, there must be heritable (genetic) variation for that trait, and, second, that the inheritance of life-cycle traits is generally quantitative rather than Mendelian in nature. Because life-history traits are directly associated with, and may be components of, fitness, it has long been held that selection, in maximizing fitness, should drive genetic variability for fitness traits to vanishingly low or zero levels above what could be accounted for by mutation alone (Fisher 1958; Falconer 1981). Much of the impetus of the genetic approach therefore revolves around explaining the persistence of phenotypic and genetic variation for life-history traits in laboratory and natural populations.

The second approach examines the phenotypes of conspecific or closely related insects across ecological gradients. By restricting analysis to closely related insects, one presumes that similar phylogenetic and/or ontogenetic constraints hold across populations. Phenotypic variability among populations therefore should represent a response to recent selection in those known, contrasting habitats rather than ancient selection in unknown environments for entirely different "bauplans". In some studies, the genetic underpinning of intra- and/or interpopulation variation are known. In other studies, the connection between genetic change and phenotypic evolution of life-cycle traits is not known but is at least potentially determinable.

The third approach makes comparisons among taxa independently of their

relatedness and no pretence is made about the possibility of genetic connections. Rather, the focus is on the question of whether specific suites of life-history traits among broad taxa are generally, even if not universally, associated with specific habitats. Thus, along spatial and temporal ecological gradients, certain patterns of life-history syndromes begin to emerge.

Below, I shall discuss the contributions of the papers in this volume to these three levels of approach and the ways in which the levels are, and should continue to be, connected. Finally, I shall pose a series of questions whose pursuit might occupy our future endeavours until these questions are resolved or it is established that they are intractable and new questions supplant them.

14.2 Maintenance of Genetic Variability for Fitness Traits

Additive genetic variance (narrow-sense heritabilities) of life-history traits (high fitness components) persists over a wide variety of insects. Heritability for life-history traits may, generally, be less than heritability for morphological, physiological and behavioural traits, but it is consistently non-zero (Roff, Chap. 1; Istock 1982; Roff and Mousseau 1987; Mousseau and Roff 1987). Very generally, there is no longer a paradox between presumed lack of genetic variation and observed life-cycle variation. Sufficient genetic variation persists in present-day insect populations to explain the remarkable variety of life-cycle traits and syndromes presented in this volume.

The proposition that selection should drive genetic variation of high fitness traits to vanishingly low levels is now a straw man and no longer an appropriate focus for primary enquiry. The question does remain as to the processes that maintain such variation despite putative selection to the contrary. The answers to this question are still forthcoming and chapters in this volume have given us good direction.

Genetic variability for high fitness traits can be maintained above levels explained by mutation by frequency-dependent selection and/or environmental heterogeneity (Roff, Chap. 1). The effect of environmental heterogeneity in maintaining genetic variability may be enhanced through mechanisms discussed by Taylor (Chap. 9) and Shorrocks (Chap. 12). Taylor shows that the time for the mean and standard deviation of a phenotype to converge on the long-term optimum in response to stabilizing selection rapidly increases to hundreds of generations when environments fluctuate and are autocorrelated. When the mean of the optimal phenotype is also changing, gene frequencies may be perpetually chasing an elusive optimum. One can then ask whether populations in autocorrelated, seasonal environments whose mean varies over decades or centuries ever approach genetic equilibrium. Shorrocks (Chap. 12) extends his models of a "probability refuge" that serves to maintain potentially competing species in a community to include the interaction of potentially "competing" genes in a patchy environment. Shorrocks' models are especially enlightening because each genotype alone achieves the same fitness in all patches but fitness does vary according to the other genotypes in that patch. Consequently, even in the absence of multiple-niche polymorphism (Levene 1953; Haldane and Jayakar

1963; Levins and MacArthur 1966) aggregation of genotypes in transient, patchy environments can maintain high levels of genetic diversity or retard the elimination of inferior alleles. The combined effects of fluctuating, autocorrelated environments and aggregation of genotypes in patchy, ephemeral environments might then maintain high genetic diversity indefinitely.

Both Roff (Chap. 1) and Rose et al. (Chap. 2) propose that genetic variability of high fitness traits persists because of antagonistic pleiotropy. Rose et al. ask, in the most rigorously controlled laboratory populations of *Drosophila melanogaster*, whether antagonistic pleiotropy *can* account for trade-offs between adult longevity and reproductive effort early in adult life. Their answer demonstrates convincingly that antagonistic pleiotropy is real but at the same time, is not "exclusively important". Examination of a variety of life-histories in *D. melanogaster* and *Oncopeltus fasciatus* by Roff (Tables 1.3 and 1.4) would appear to confirm this conclusion.

The comparisons made by Roff (Chap. 1) illustrate several problems that must be confronted. First, genetic correlations with respect to fitness may be positive in recently inbred lines (Rose 1984) or when the determination of genetic correlations is made in environments that are different from the environment in which the organism underwent selection (Service and Rose 1985). Before we can entirely legitimize the comparative signs of genetic correlations, we need to answer two questions. First, what level of inbreeding and, second, how great a departure from the natural environment are likely to produce bias in the estimation of genetic correlations? Rose et al. (Chap. 2) used populations of *D. melanogaster* reared under the same laboratory conditions for over 250 generations. This technique permitted populations to approach genetic equilibrium and was essential for rigorously testing ways in which genotypes *can* be organized but says little about how genotypes *are* organized in natural populations. To avoid effects of novel environments, Bradshaw and Holzapfel (Chap. 3) looked for trade-offs (Fig. 3.11) in life-history traits among populations of pitcher-plant mosquitoes reared in the water-filled leaves of intact pitcher plants under conditions of near-natural light, temperature and feeding. Eventually, this technique will reveal a great deal about the phenotypic and genetic variation and covariation of traits within and between natural populations. The vast majority of insects do not, however, dwell in such highly circumscribed habitats that are transposable to controlled but near-natural conditions in the laboratory. How great an abstraction from nature are the laboratory cultures referenced in Roff's Tables 1.3 and 1.4? Would evidence for antagonistic pleiotropy have been more prevalent if rearing conditions were more natural? There are as yet no examples that I know of that compare genetic correlations over a series of environments from natural to artificial. Such studies are needed to provide a link between the work of Rose et al. (Chap. 2) and other studies, exemplified by Roff (Chap. 1), Scott and Dingle (Chap. 4), and Solbreck et al. (Chap. 11).

14.3 The Genetic Connection in Life-History Syndromes

The majority of chapters in this volume use a comparative approach to the evolution of life-cycle traits. The link between the existing patterns of insect life-

cycles and the evolutionary sequence of genetic events is generally tenuous at best. At some point, this connection between genetic change and phenotypic evolution should be made wherever possible.

The gaps in the "genetic connection" occur at several levels. Rose et al. (Chap. 2) have shown clearly that antagonistic pleiotropy can and does exist in laboratory populations of *D. melanogaster*; Bradshaw and Holzapfel (Chap. 3) have shown a lack of detectable coevolution among demographic traits and between demographic and phenological traits in adjacent and widespread natural populations of *Wyeomyia smithii*. As yet there is little common ground. Bradshaw and Holzapfel do not show whether the underlying genetic correlations *within* populations are parallel to, or diverge from, the pattern *among* populations. Genetic correlations are usually interpreted as imposing a cost to the adaptive evolution of life-history traits (Hegmann and Dingle 1982) and the correlated response of a variety of traits to direct selection on body size in *O. fasciatus* (Palmer and Dingle 1986) is predictable from the underlying genetic variance–covariance matrix. Over longer-term selection, linkage groups may dissociate and this dissociation can lead to an accelerated response to selection (Falconer 1981, pp 195–196). Genetic correlations can differ in nearby (Groeters and Dingle 1987) or distant populations (Berven and Gill 1983). Just as selection could favour the evolution of co-adapted gene complexes that can form tightly linked "supergenes" (Ford 1971), so also could selection break up these linkage groups. Pleiotropic effects can be mediated by a single hormone. The titre of juvenile hormone is probably the common link between migration behaviour, wing muscle development, and wing development in gerrid (Roff, Chap. 1) and lygaeid (Solbreck et al., Chap. 11) bugs. Threshold titre could, however, vary independently, thus dissociating any one or two of these traits. The focus of natural selection can be a single trait, a group of genetically correlated traits, and/or the degree of genetic correlation itself (Bradshaw 1986). Clearly, genetic correlations do impose a "cost of correlation" (Dingle 1984; Palmer and Dingle 1986) in the immediate response to selection over a few generations, but we do not know whether genetic correlations impose significant impediments to the divergence of life-cycle traits over the range of a single species (Bradshaw and Holzapfel, Chap. 3; Scott and Dingle, Chap. 4; Masaki, Chap. 7; Solbreck et al., Chap. 11; Wipking, Chap. 13).

14.4 Emergent Life-Cycle Patterns

At some point in the broadening analyses of insect life-histories, making a genetic connection will become extremely difficult, if not impossible. Brown (Chap. 10), for example, looks for patterns of herbivore life-histories that change with plant successional stage. If one population of a single species persists through several successional stages *and* life-cycle traits of this population could be serially assessed without placing them in novel environments, then the genetic connection could, conceivably, be made. But, in any two given species the life-cycle traits during successional stages might change in opposite directions. By themselves, these two species would not tell us much about life-cycle strategies during succession but a survey of a broad number of taxa might. Thus, even without the

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genetic connection, the question of how life-cycle traits among diverse taxa covary along environmental gradients or over successional time remains legitimate. The emergent patterns then tell us something about life-cycles that facilitate or are necessary for existence in the particular spatial or temporal environments.

Without a genetic connection, we must be especially wary of ascribing cause and effect to emergent patterns. Do life-histories pre-ordain the suite of habitats in which an insect can sustain positive fitness or do life-histories of insects evolve continually to maintain or improve fitness in the habitats that they occupy? Brown's study (Chap. 10) shows an association of rapid dispersal ability among the insects prevalent at early rather than later stages of plant succession. This dispersal ability is then likely to be part of a broader syndrome of traits involving development time, growth rate and reproductive allocation (Roff, Chap. 1; Scott and Dingle, Chap. 4; Solbreck et al. Chap. 11). Insects capable of dispersing persist throughout succession but their frequency falls with advancing successional stages. Does this decline in ability to disperse mean that older successional communities select for non-dispersers or that, being capable of dispersal, dispersers simply leave and seek fresh habitats that they are more capable of exploiting? It is clearly exciting to think about a dynamic process such as coevolution or the habitat templet (Southwood 1977) driving the evolution of life-histories. It is much more mundane but sometimes more appropriate to think about organisms occupying habitats where they are able to make a living and then, when they cannot, moving on.

Focusing on mobile insects that tend to be generalists may provide a biased viewpoint of cause and consequence between the habitat and life-cycle syndromes, since host-plant specificity and reduced dispersal ability both increase with successional age (Brown, Chap. 10). Indeed, we can ask whether habitat-driven evolution is more intense among specialized, non-dispersers than among generalized, dispersal-capable insects. Even if generally true, counter-examples in this volume argue against it being universally true. Solbreck et al. (Chap. 11) found that wing-reduced, polyphagous lygaeids have larger body size and lay fewer, larger eggs than the monomorphic long-winged, monophagous lygaeids; by contrast, Gilbert (Chap. 6) found that among saprophagous syrphids, generalists are smaller and lay more, smaller eggs than specialists. There is therefore no universal tendency for dispersers to be more generalized as compared to non-dispersers. Finally, Berenbaum (Chap. 5) describes opportunistic host transfer to Psoralea (Leguminosae) by furanocoumarin-tolerant specialist papilionids and oecophorids that have otherwise probably coevolved with the Umbelliferae. Thus, even highly specialized, coevolved insects may opportunistically exploit novel hosts when they are available.

I do not despair at the variation in pattern of generalists versus specialists between lygaeids and syrphids. Rather, there is tremendous opportunity here to identify even more universal patterns by finding the common environmental causality between these two orders of insect. If the common ground remains elusive, I would make a plea that we preserve the inconsistency as a paradox rather than dismissing the differences to "phylogenetic constraints", a phrase that makes us think we know something but in reality may be simply a euphemism for "lygaeids and syrphids do it differently".

It is also important to know where answers are not going to be forthcoming. Berenbaum (Chap. 5) argues that even if host biochemical toxins and herbivore

tolerances generate identical cladograms, there may still be no way to distinguish opportunistic colonization from mutual descent as an evolutionary process. Here, as Berenbaum's own work has shown, establishing the connection between genetic change and phenotypic evolution may be very necessary.

There are emergent patterns in insect life-history syndromes. These patterns are well illustrated in the chapters by Brown (Chap. 10), Gilbert (Chap. 6), and Solbreck et al. (Chap. 11). Emergent properties cannot and should not imply underlying genetic and/or physiological causality. Yet, emergent properties provide patterns of life-history variation across habitats and serve as analogues of models about selection in these habitats. Present emergent properties can therefore serve as guidelines for future testing of their predictions and their underlying assumptions by using reductionist approaches similar to those discussed above. Thus, lygaeid and gerrid life-cycle syndromes can be broken down from the diapause–migration flight (behavioural level) to the wing length and wing musculature versus ovarian or forelimb development trade-off (physiological level) or even to the mode of action of juvenile hormone on different developing tissues and lipid mobilization (cellular-biochemical level). Present emergent properties may just as well be refined, without implying genetic or physiological mechanisms, by continuing an expansionist approach in the future. Do emergent life-history patterns persist across taxa or across habitats? What is the common ground between wing-reduced lygaeids and saprophagous syrphids? Do similar life-history patterns during plant succession apply to carnivores, to detritivores, or in different climates, on different continents, or in different plant communities?

14.5 Where Do We Go From Here?

Life-history traits are the emergent phenotypes of underlying genotypes that may or may not respond to varying environments. It would seem to me to be a fruitful area to consider the physiological underpinnings of life-cycle syndromes, as shown in a general sense by Rose et al. (Chap. 2). Juvenile hormone has been implicated as a pivotal hormone in the life-cycles of Hemiptera (Roff, Chap. 1; Scott and Dingle, Chap. 4; Solbreck et al., Chap. 11). The Orthoptera considered by Scott and Dingle (Chap. 4) and by Masaki (Chap. 7) and the Lepidoptera considered by Wipking (Chap. 13) would appear to be good potential groups for similar studies. These authors all consider traits known to be under close hormonal control. What would be the various correlated responses to selection for low/high titre of hormones during development or for advanced or delayed production of the same titre? Answers to these questions would tell us the multitude of traits within a single life-cycle but both within and between stadia that could be affected by the timing and titre of single or a few hormonal events.

At the population level, there is good evidence that genetic correlations impose a "cost of correlation" in the immediate response to selection (Palmer and Dingle 1986). However, we do not know the extent to which genetic correlations have facilitated or impeded the adaptive divergence of even a single species. Observing the response to selection over the short term in nature is going to present several

problems in interpretation. Natural environments will probably impose fluctuating selection so that detection of long-term optima will be elusive within two or tens of generations because of the "curse of autocorrelation" (Taylor, Chap. 9). Observed responses to short-term selection in nature are also likely to reconfirm the importance of genetic correlations as a constraint. Geographically disparate populations of the same species provide a special opportunity to examine the end points of longer-term selection. Do phenotypic correlations between disparate populations reflect static or changing genetic correlations for the same traits? When genetic correlations change among populations, do mean phenotypes change in the same way? Answers to these sorts of question may be forthcoming from a variety of ongoing studies including those of Roff (Chap. 1), Bradshaw and Holzapfel (Chap. 3), Scott and Dingle (Chap. 4) and Solbreck et al. (Chap. 11). Two others studies provide opportunities to examine life-history divergence across a sub- or sibling-species distance. Masaki (Chap. 7) outlines the responses to temperature and photoperiod that enable a subtropical cricket to enter an opportunistic diapause that is distinct from its temperate sibling-species. Since the two species are nearly identical morphologically, it is their diapause response to climate that distinguishes them. Similarly, Wipking (Chap. 13) describes contrasting life-cycle phenologies in two sibling-species of *Zygaena* on continental Europe where an additional aestivation (waiting) period is the major difference between the two species. Along with *W. smithii* (Bradshaw and Holzapfel, Chap. 3), there is a tremendous opportunity here to examine the genetic covariation within and between life-cycle syndromes involved in direct development (demographic traits) and syndromes involved in dormancy or migration (phenological traits) among three very different orders of insect.

In total agreement with Roff (Chap. 1), I would emphasize that "what is urgently required are empirical analyses of the genetic structure of ecologically important characters". I would like to add, however, that we should invest the enormous amount of required effort into species whose ecology is reasonably well known. "Ecological importance" is likely to vary enormously between species, even those with convergent life-styles. Host–pollinator mutalisms (Addicott et al., Chap. 8) provide a prime example. The constraints and opportunities operating on the fig wasp–fig interaction are far different from those operating on the yucca moth–yucca interaction. The constraints and opportunities affect the timing and variation of development and dispersal and also affect the degree of host–pollinator fidelity even though both systems could be classified as tight, obligate mutualisms.

The ecology of the species becomes even more important when studies are made of emergent life-cycle patterns. Species need to be classified as disperser/non-disperser, generalist/specialist, competitor-limited/free, uni-/multivoltine, egg/immature/adult overwintering stage, or predator/omnivore/detritivore/herbivore (Gilbert, Chap. 6; Brown, Chap. 10; Solbreck et al., Chap. 11). This classification is essential in determining how these life-cycle traits change across spatial and temporal habitats. At best, misclassification contributes to error and patterns that do, in fact, exist, may be missed. Worse, misclassification could result in the perception of a significant pattern when, in fact, one does not exist or is opposite from the one perceived.

To answer the initial question of where do we go from here, I would conclude that we must continue to integrate the three levels of approach described in this chapter. This integration will enable us to answer the following questions.

1. How does the underlying biochemistry contribute to the physiology that orchestrates the seasonal and developmental traits that we measure?
2. How does the genetic architecture of these traits vary between populations of the same and closely related species along ecological gradients?
3. Has the diversity of life-cycle traits that we see among closely related populations arisen because of, or despite, the underlying genetic architecture? What is the span in evolutionary time or in taxonomic level of genetic constraint and/or genetic facilitation?
4. How are life-cycle traits integrated into the ecology of insects? Are the fitness traits perceived by the investigator truly crucial to the insects in nature?
5. What are the major emergent patterns of insect life-cycles and how do we reconcile the exceptions?
6. Do environments direct the evolution of life-history or do established life-histories determine the ecology of a population, species or higher taxon?

References

Berven KA, Gill DE (1983) Interpreting geographic variation in life history traits. Am Zool 23: 85–97

Bradshaw WE, (1986) Pervasive themes in insect life cycle strategies. In: Taylor F, Karban R (eds) The evolution of insect life cycles. Springer, Berlin Heidelberg New York, pp 261–275

Dingle H (1984) Behavior, genes, and life histories: complex adaptations in uncertain environments. In: Price PW, Slobodchikoff CH, Gaud WS (eds) A new ecology: novel approaches to interactive systems. Wiley, New York, pp 169–194

Falconer DS (1981) Introduction to quantitative genetics. Longman, London New York

Fisher RA (1958) The genetical theory of natural selection. Dover Publications, New York

Ford EB (1971) Ecological genetics. Chapman & Hall, London

Groeters FR, Dingle H (1987) Genetic and maternal influences on life history plasticity in response to photoperiod by milkweed bugs (*Oncopeltus fasciatus*) Am Nat 129: 332–346

Haldane JBS, Jayakar SD (1963) Polymorphism due to selection of varying direction. J Genet 58: 237–242

Hegmann J, Dingle H (1982) Phenotypic and genotypic covariance structure in milkweed bug life history traits. In: Dingle H, Hegmann J (eds) Evolution and genetics of life histories. Springer, Berlin Heidelberg New York, pp 177–188

Istock CA, (1982) The extent and consequences of heritable variation in fitness characters. In: King CR, Dawson PS (eds) Population biology: retrospect and prospect. Columbia University Press, New York, pp 61–96

Levene H (1953) Genetic equilibrium when more than one ecological niche is available. Am Nat 87: 331–333

Levins R, MacArthur R (1966) The maintenance of genetic polymorphism in a spatially hetero-geneous environment: variations on a theme by Howard Levene. Am Nat 100: 585–589

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Palmer JO, Dingle H (1986) Direct and correlated responses to selection among life history traits in milkweed bugs (*Oncopeltus fasciatus*). Evolution 40: 767–777

Roff DA and Mousseau TA (1987) Quantitative genetics and fitness: lessons from *Drosophila*. Heredity 58: 103–118

Rose MR (1984) Genetic covariation in *Drosophila* life history: untangling the data. Am Nat 123: 565–569

Service PM, Rose MR (1985) Genetic covariation among life history components: the effect of novel environments. Evolution 39: 943–945

Southwood TRE (1977) Habitat, the templet for ecological strategies? J Anim Ecol 46: 337–365

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